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THE EVOLUTION OF THE CIRCULATORY ORGANS.

BY W. C. CAHALL.

IN the March (1890) number of the AMERICAN NATURALIST I attempted to marshal the evidences furnished by the teeth in support of the hypothesis of evolution. Any other organ or group of organs could have been selected and found equally rich in evidences of a similar import. But none, perhaps, approach quite so nearly to a demonstration, as the beautiful series of cardiac organs met with by the comparative anatomist in his study of zoology.

Origin of Circulatory Organs.—In the lower forms of life, the Protozoa, where no differentiation of structure has yet taken place, the organs of circulation, like those of digestion, are not needed, for every part of the organism performs its own act of digestion and absorption of nutriment. Where a digestive tube is formed, as in the Hydra, the digested food passes by direct absorption into the tissues of the body. In the same group with the Hydra, the Cœlenterata, there are species where from the digestive tube radiate numerous canals which distribute the chyme to every part of the body.

In other species of the same group we see slight but significant and progressive changes in these canals. This "gastro-vascular system," as it has been called, is the first approach to *circulation* we meet with in ascending the animal scale. It is for all practical purposes an efficient circulatory system, yet it is, structurally, nothing more than an amplification of the digestive tract.

The first approach to independence of the organs of circulation from those of digestion is within the Vermes or worms. They have walls and are blood-vessels indeed, since they have a regular circulation of a blood-fluid. A simpler kind is that of some Nemertina, where the main trunks are three long canals connected by transverse shorter ones (Fig. 1).

In Fig. 2 is represented a more complicated system as found

in a higher class of the Vermes, which are furnished with both dorsal and ventral vessels, with pairs connecting them at regular intervals. One or more of these transverse vessels may be

enlarged and pulsatile. While at other times the dorsal vessel itself acts as a heart. In this last we are to trace the origin of the heart of both anthropods and vertebrates.

In the one great group, the Mollusca, there are four types whose several hearts furnish as clear a demonstration of the evolution of an organ as could well be desired. Some reader, unacquainted with comparative anatomy, may even imagine the sketch (Fig. 3) an ideal one by some over-zealous evolutionist, made to confirm his theory; but myriads of these hearts are throbbing to-day as living contradiction to this suspicion. *A* represents a dorsal vessel and transverse trunks of the worm, such as we have already seen in Figs. 1 and 2. *B*.

Here we have the single, straight, pulsating ventricles (*v*) with the branching auricles (*a*), as found in the *Nautilus*. In *C* we have a similar organ of the *Loligo*, with the auricles

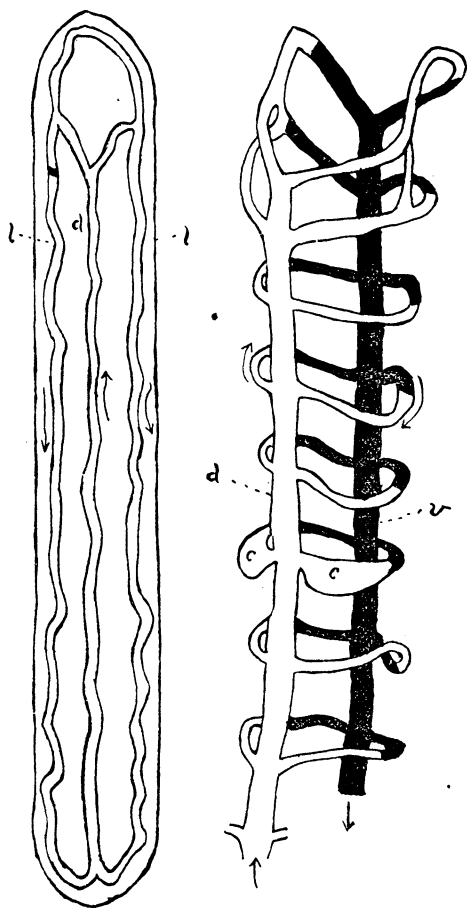


FIG. 1.—Diagram of the vascular system of *Nemerita*: *d*, dorsal longitudinal trunk; *l*, lateral vessels. The arrows indicate the direction of the stream of blood. After Gegenbaur.

FIG. 2.—Vascular system of *Sænrus variegata*: *d*, dorsal vessel; *v*, ventral vessel; *c*, heart-like enlargement of a transverse. The arrows indicate the direction of the current of blood. After Gegenbaur.

tricles (*v*) with the branching auricles (*a*), as found in the *Nautilus*. In *C* we have a similar organ of the *Loligo*, with the auricles

reduced to two. *D* is a diagram of the heart of the Octopus, where for the first time we meet with the organ bent upon itself *E* represents the heart of ventricle and single auricle of the Gastropod, the extreme of development in one direction.

The heart of the fishes likewise consists of two cavities, one auricle and one ventricle, but this is not to be homologised with the two cavities of the molluscan heart. In the Mollusca the auricle receives aërated blood from the respiratory organs, and passes it to the ventricle, which propels the oxygenated blood throughout the body, thus forming a systemic circulation. The Mollusca have no capillaries save in the respiratory organs, so that the blood, after leaving the arteries, flows through canals or lacunæ within the substance of the body. In the fishes, on the contrary, the two cavities convey only venous blood, thus performing the same function as the right side of the heart of mammals. The deoxygenated blood is gathered up from all parts of the body, and conveyed by the veins to the auricle, thence to the ventricle, which organ forces it through the truncus arteriosus into the capillaries of the gills, where the blood is oxygenated by the free oxygen held by the water. The now aërated blood is gathered up by the radices aortæ, and the dorsal aorta distributes it throughout the body (Fig. 4.) This figure should be compared with Fig. 2, when it will at once be seen, after making allowances for the inverted position of the worm, that the heart of the fish corresponds with the dorsal vessel of that figure, the gill circulation to the transverse vessels of the worm, and the ventral vessel of the one to the dorsal aorte of the other. The resemblances to the Mollusc are largely those of analogy; those to the Annelid, those of true homology.

In the reptiles we see a further development of this central engine of life. Here we have two auricles with one ventricle. The auricle of the fish has had a septum placed down its middle, forming two cavities. In some lower forms this septum is incomplete, but in typical reptiles it is complete. The ventricle also has the rudiments of a septum. Indeed, in some of the higher reptiles, the crocodile for instance, the separation is almost perfect, thus approaching the normal condition of the bird and mammalian

heart. The impure blood which has passed through the system is conveyed to the right auricle, while the left auricle receives the oxygenated blood from the lungs. Thus pure and impure blood become mixed in the ventricle. There are two aortic arches arising from the ventricle, one from the right side and the other from the left. The blood coming through the right aortic arch, now become the pulmonary artery, flows through the pulmonary artery to the lungs, while that entering the left aortic arch is carried throughout the system (Fig. 5).

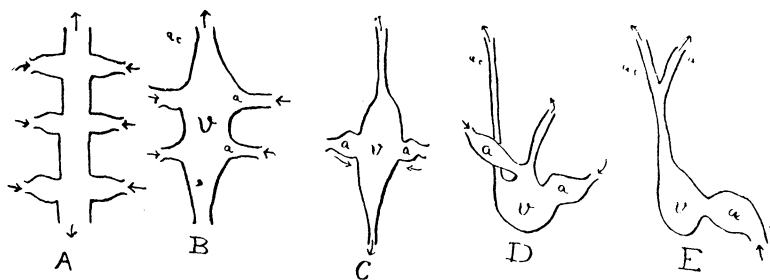


FIG. 3.—CIRCULATORY CENTERS OF MOLLUSCA.—*A*, dorsal and transverse trunks of worm; *B*, heart and auricles of Nautilus; *C*, heart and auricles of Loligo; *D*, heart and auricles of Octopus; *E*, heart and auricles of Gastropod; *v*, ventricle; *a*, auricle; *ac*, arteria cephalica; *a*, arteria abdominalis. The arrows show the direction of the current of blood. After Gegenbaur.

The heart of the bird and of mammals consists of two auricles and two ventricles. The venous blood is gathered up from all parts of the body and emptied into the right auricle, whence it flows through the tricuspid valves into the right ventricle, which by its forcible contraction drives the blood through the pulmonary artery into the lungs. Here the aërated blood is returned to the heart again through the pulmonary veins to the left auricle, thence through the mitral valves to the left ventricle, which sends it bounding throughout the system. There are in the bird and mammal, then, two distinct hearts; the right half, like the heart of the fishes, carrying only venous blood, and the left side, like the heart of the Mollusca, carrying only arterial or aërated blood, while the heart of the reptile is an intermediate organ between the simple apparatus of the fishes and the compound heart of the Mammalia (Fig. VI.).

Thus we have traced, by easy and gradual steps, the complete evolution of the simple pulsating vessel of the Annelid unto the marvelously perfect organ of man. We have seen how the one pulsating tube has divided into two by a partial and then a perfect septum, into an auricle and a ventricle, and then have seen these cavities, by a partition more and more complete, separated into four distinct cavities. Yet all this is done with but slight alterations of preëxisting structure, and without a link in the chain missing. This is an argument approaching a demonstration, and must appeal to all candid minds. To those who might object that even the slight changes could not be made without the destruction of the animal or species, I would instance the transformation of every tadpole into a frog. Surely no one will assume that tadpoles are changed now into a frog by any power save that residing in natural laws. Yet the changes are profound.

The heart of a tadpole is practically that of a fish, having one auricle and one ventricle, and the animal breathes by gills; yet a frog has two auricles and a ventricle, and breathes by lungs. Here we see changes equivalent to the transformation of a fish into a reptile. And among reptiles we meet with hearts with every degree of partition, until in the crocodile the heart is partitioned off very nearly the same as in birds and mammals. In the development of the heart in embryos of birds and mammals we find the organ passing through the conditions found permanently in lower forms. A distinguished comparative anatomist thus outlines the development of the embryo chick: "The first rudiments of the heart appear about the 27th hour, and is a mass of cells, of which the

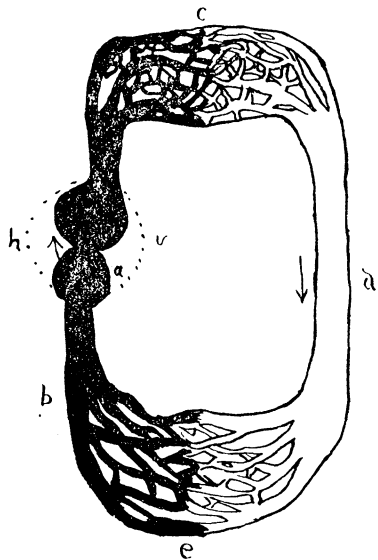


FIG. 4.—CIRCULATION IN FISHES.—*h*, heart, enclosed in pericardium; *a*, the auricle; *v*, the ventricle; *c*, the capillary action in the gills; *d*, the dorsal artery; *e*, the systemic capillaries; *b*, the veins.

innermost soon break down, so as to form a tubular cavity; for some time it is simple and undivided, extending, however, through nearly the whole length of the embryo. No motion of fluid is seen in the heart or vessels until the 38th or 40th hour. When the heart, which may be considered analogous at this period to the dorsal vessel of the Annelida, first begins to pulsate, it contains only colorless fluid mixed with a few globules. Between the 40th and 50th hours a separation in its parts may be

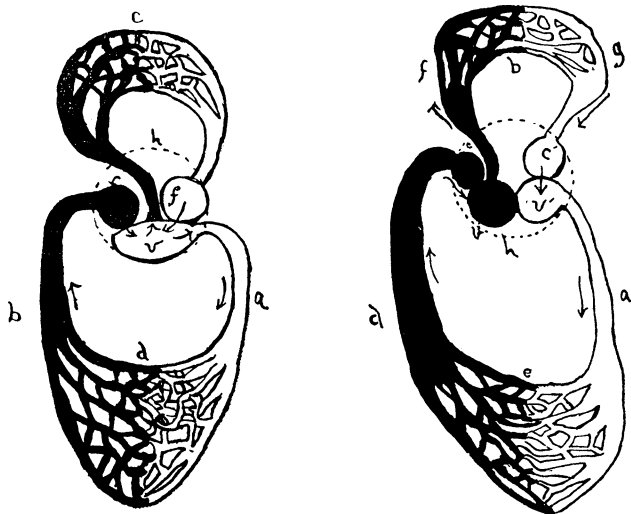


FIG. 5.—CIRCULATION IN REPTILES.—*h*, heart, enclosed in pericardium; *ff*, right and left auricles; *v*, single ventricle; *a*, aorta; *v*, vena cava; *c*, smaller circulation; *d*, greater circulation.

FIG. 6.—CIRCULATION IN MAMMALS AND BIRDS.—*h*, heart; *v*, right ventricle; *v'*, left ventricle; *c*, right auricle; *c'*, left auricle; *a*, aorta; *d*, vena cava; *e*, greater circulation; *f*, pulmonary artery; *g*, pulmonary veins.

observed, which is effected by a constriction round the middle of the tube; and the dilation of the posterior portion becomes an auricular sac, and that of the anterior a ventricular cavity. Between the 50th and 60th hours the tube of the heart becomes more and more bent together until it is doubled, so that this organ becomes much shorter relatively to the dimensions of the body, and is more confined to the portion of the trunk to which it is subsequently restricted. About the same time the texture of the auricle differs

considerably from that of the ventricle; the auricle retaining the thin and membranous walls which it at first possessed, while the ventricle has become stronger and thicker, both its exterior and interior surfaces being marked by the interlacement of muscular fibres, as in the higher Mollusca. About the 65th hour the grade of development of the heart may be regarded as corresponding with that of the fish, the auricle and ventricle being perfectly distinct; but their cavities are as yet quite single. During the fourth day the cavities of the heart begin to be divided, for the separation of the right and left auricles and ventricles. About the 80th hour the commencement of the division of the auricle is indicated, externally, by the appearance of a dark line on the upper part of its wall; and this, after a few hours, is perceived to be due to a contraction, which, increasing downwards across the cavity, divides it into two nearly spherical sacs. The division of the ventricle commences *some time before* that of the auricle, and is effected by a sort of duplicature of its walls. At last, however, the division is complete, and the interventricular septum becomes continuous with the interauricular, so that the heart may be regarded as completely a double organ. The progressive stages presented in the development of this septum are evidently analogous to its permanent conditions in the various species of reptiles. In the heart of mammals (embryo) the same changes take place, but more slowly. Soon after the septum of the ventricles begins to be formed in the interior, a corresponding notch appears on the exterior, which, as it gradually deepens, renders the apex of the heart double.

“This notch between the right and left ventricles continues to become deeper until about the eighth week in the human embryo, when the two ventricles are quite separated from one another, except at their bases; this fact is very interesting from its relation with the similar permanent form presented by the heart of Dugong.

“At this period the internal septum is still imperfect, so that the ventricular cavities communicate with each other, as in the chick, on the fourth day. After the eighth week, however, the septum is complete, so that the cavities are entirely insulated; whilst at the same time their external walls become more connected towards

their base, and the notch between them is diminished; and at the end of the third month the ventricles are very little separated from one another, though the place where the notch previously existed is still strongly marked.

"In the state of the circulatory system in the early embryo, where the heart is as yet but a pulsating enlargement of one of the principal trunks, and the walls of the vessels are far from being complete, we have the representation of its condition in the higher Radiata, and in the lower Articulata and Mollusca. In the subsequent division of the cardiac cavity into an auricle and ventricle an advance is made, corresponding to that which we encounter in passing from the Truncata to the higher Mollusca. And when the branchial arches are formed, which enclose the pharynx and meet in the aorta, the type of the fish is obviously attained, and at a subsequent period the condition of the heart and great vessels presents a strong general resemblance to that of the typical reptiles."

Even at birth the true mammal heart is still incomplete, for there is an opening in the septum between the right and left auricles called the *foramen ovale*, which does not entirely close until after birth, and not in all cases then, leaving the child so formed in a condition almost certain to lead to early death. Does not this opening, which is of no use to foetus or child, seem more likely to be the result of a general evolution, rather than of a special creation of a useless and oftentimes a harmful accident?

There is also, in the foetal circulation, a connecting vessel between the pulmonary artery as it emerges from the right ventricle and the aorta as it leaves the left ventricle. This *ductus arteriosus* soon becomes obliterated after birth, so that man has only temporarily what is persistent through life in the reptile.

The peculiar relation of the valves of the veins to the vessels they occupy in man has furnished Dr. S. V. Clevenger, of Chicago, the material for a striking argument for the evolutionary origin of man. (See AMERICAN NATURALIST, Vol. XVIII.)

The veins which return the blood to the heart against gravity, as in the legs and arms, are supplied with valves which allow the

blood to flow upward, yet close and hold the column of blood upon any tendency to regurgitate.

Now this writer claims that the valves of the veins have not yet become accommodated to the upright position of man, for there are several instances in man where the persistence of the valves in certain veins are not only useless for their original purpose, but by their position are actually obstructive to the return of the blood to the heart. He asks, What earthly use has a man for valves in the intercostal veins which carry blood almost horizontally backward to the azygos veins?

When recumbent they are actually a detriment to the free flow of blood. The inferior thyroid veins, which drop their blood into the innominate, are obstructed by valves at their junction. Two pairs of valves are situated in the external jugular and another pair in the internal jugular, but in recognition of this uselessness they do not prevent regurgitation of blood nor liquids from passing upwards. Where apparently most needed, such as venæ cavæ, spinal, iliac, hemorrhoidal, and portal, there are none. The azygos veins have imperfect valves; their rudimentary condition suggests that they may be of recent origin. Now place man on "all fours," and these anomalies disappear. The veins which in man erect do not need valves will be seen to need them against gravity when on "all fours," and as they are found in all four-footed animals; and where, in man erect, those veins which need valves but have them not, when on "all fours" will not need them. Valves in hemorrhoidal veins in quadrupeds would be out of place, yet their absence in man sacrifices many lives and produces untold suffering. It is difficult to escape from the consequences of Dr. Clevenger's logic.

Malformations.—Cyanosis results from the *foramen ovale*, which establishes a communication between the auricles, remaining open after pulmonary respiration had been established, a condition permanent in the crocodile. An arrest of development at an earlier period may cause still greater imperfections in the formation of the heart. Thus, the septum of the ventricles is sometimes found incomplete, the communication between the cavities usually occurring in the part which is last formed, and

which in most reptiles remains open. A still greater degradation in its character has been occasionally evinced, for several cases are now on record in which the heart has preserved but two cavities, an auricle and a ventricle, thus corresponding with that of the fish; and in one of these instances the child has lived for seven days, and its functions had been apparently but little disturbed.

The bifid character of the apex, which presents itself at an early period of the development of the mammalian heart, and is permanent in the Dugong, sometimes occurs as a malformation in the adult subject, evidently resulting, like the others which have been mentioned, from an arrest of development.

The Blood.—The form-elements of the blood itself indicate a parallel evolution with that of the heart and vessels. In the Vermes, where the vascular system is first separated from the digestive tract, the liquid contents known as the blood are generally colorless, occasionally green or reddish in color, and the form-elements are of but slightly different cells. The blood of the Echinoderma (sea-stars and sea-urchins) is of clear or slightly opalescent color, and the form-elements are simple cells.

The blood of the Arthropoda is generally colorless; only in a few insects is it greenish or reddish; even then the color is due to the plasma and not to the cells, which are colorless and of variable size and form, and absent entirely in some of the lower forms, as the Crustacea. The blood of the Mollusca is generally colorless, sometimes bluish, violet, or green; only in one species is the blood red, and then from the plasma, for the blood-cells are simple, undifferentiated, and always colorless.

The blood of crabs and other Crustacea has been proved by M. Fredericq to contain the same saline elements and the same strong and bitter taste as the waters they inhabit. But the blood of sea-fishes is very different. It has not the same constitution as that of the crabs, and shows a marked superiority over them. In fact, the character of the blood-fluid of the invertebrates is strikingly similar to the lymph of the higher vertebrates where the lymphatic and vascular systems are separated. In both, the cells are simple and undifferentiated, colorless, opalescent, or pink.

Even after we enter into an examination of the vertebrates we will meet with a species, and, as we should be led to expect from an evolutionary standpoint, it happens to be of the very lowest class of the vertebrates, the *Amphioxus*, where the blood-fluid is colorless, and its form-elements are very small, indifferent cells. It is also significant that here also the lymphatic system is not entirely distinct from the vascular system.

But in all other vertebrates, after we leave this lowest class, we shall find the two systems separate, and the blood color red. While the blood is uniformly red, the form-elements of each of the great families of the vertebrates are distinctive and characteristic. The color of the blood now depends upon the coloring matter contained in the blood-cells, and not, as in the few instances of colored blood of the invertebrates, upon the colored plasma. The blood-cells of all vertebrates are highly differentiated, and all contain a nucleus, save the red corpuscles of the highest, the mammals, and even here the nucleus is present in the foetal stages. The cells are generally flattened. In fishes, *Batrachia*, reptiles, and birds they are oval and biconvex, while in mammals they are biconcave. The relative quantity of blood in the higher classes of the vertebrates remains the same, yet the relative cell surface varies decidedly.

The red blood-cells are essential to respiration and as carriers of oxygen to the tissues. Fishes consume very little oxygen, and so the red blood-cells are not relatively numerous, and they are called cold-blooded animals, having a temperature but little above that of the surrounding medium. The *Batrachia* are similarly constituted, but the reptiles have some higher qualities, but still inferior to birds and mammals, which are classed as warm-blooded.

The physiological data contained herein are not the teachings of any special school of science, but the well-digested and generally accepted conclusions of the principal modern authorities on comparative anatomy,—as may be seen more in detail in such works as Carpenter's "*Comparative Anatomy*," Cope's "*Origin of the Fittest*," Gegenbaur's "*Elements of Comparative Anatomy*," Huxley's "*Anatomy of Vertebrated Animals*," and Owen's "*Comparative Anatomy and Physiology*."